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**INFLUENCE OF FOOD SUPPLY ON THE DURATION
OF THE GREGARIOUS PHASE OF A
MATERNAL-SOCIAL SPIDER, *COELOTES TERRESTRIS*
(ARANEAE, AGELENIDAE)¹**

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ABSTRACT

In spiders, modes of social organization range from solitary to communal living. The "maternal-social" spiders represent an intermediate step, where the young disperse before adulthood after a gregarious phase of variable length depending on the species. Why does social life disappear in these species? Several arguments lead us to involve trophic factors and to formulate the hypothesis that food shortages, resulting from the increase in the young's food requirements and from the limitation of the colony's prey supply, induce the spiderlings to emigrate.

To test this hypothesis, laboratory-reared colonies (mother + offspring) of the funnel-web spider *Coelotes terrestris* (Wider) were given either an ad-libitum diet, or a reduced diet. We observed that prey consumption increased with developmental age, and that under-fed colonies dispersed significantly earlier than did ad-libitum-fed colonies. The significance of such social plasticity in the evolution of spider societies is discussed.

INTRODUCTION

Taking into account the intensity, duration and complexity of intraspecific interactions, spiders appear to exhibit quite a variety of social organization, ranging from solitary to social living. Sociality is generally supposed to have originated via two different evolutionary routes (Shear 1970, Burgess 1976, 1978, Buskirk 1981): grouping of solitary individuals (Valerio and Herrero 1977), and extension of the mother-offspring association (Kullmann 1972).

Intermediate forms of social organization, called "semi-social", "periodic-social" or "subsocal" (Shear 1970, Kullmann 1972, Krafft 1979) are of special interest. By making it possible to investigate the costs and benefits of various types of organization in various ecological conditions (Buskirk 1975, Fowler and Diehl 1978, Jackson 1978, Lubin 1980, Smith 1983, Christenson 1984), these diverse forms provide insights about the possible causes and mechanisms of social evolution.

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Since Riechert's work (1976, 1978) on the territoriality of *Agelenopsis aperta* (Gertsch), the importance of trophic effects on intraspecific interactions and on social spacing has also been shown by a number of authors with other species (for a review on social spacing, see Burgess and Uetz 1982). Recently, Smith (1983) observed that in the facultatively communal uloborid spider *Philoponella oweni* (Chamberlin) "communal groups are located at sites where insects are particularly abundant. Solitary females appear to be located at sites where the insects abundance... is at the 'background level.' A similar phenomenon was observed and experimentally studied in another facultatively communal orb-weaver, the araneid *Metepeira spinipes* F.P. Cambridge (Uetz, Kane and Stratton 1982).

However, nothing is known of a possible influence of trophic factors on the "maternal-social" spiders (Burgess and Uetz 1982), i.e., those species exhibiting maternal care, with the offspring staying in a group and being fed by their mother for a variable period of time, depending on the species (Krafft and Horel 1979). The mother-offspring association represents a high concentration of individuals in a limited space. We hypothesize that the food needs of the offspring increase along with their development, and that after a lapse of time the food needs exceed the food supply, which is limited by prey abundance in the habitat and the prey catching capacity of the colony. Eventually, food shortage induces the spiderlings to disperse. Accordingly, it should be possible to modify the duration of the gregarious phase, by experimentally modifying the abundance of prey.

We chose as a model a maternal funnel-web spider *Coelotes terrestris* (Wider), belonging to a family (Agelenidae) which includes typical solitary species as well as two highly social species: *Agelena consociata* Denis (Darchen 1965, Krafft 1970) and *Agelena republicana* Darchen (Darchen 1967).

Considering the relationship between social structure and trophic factors, we studied the effect of prey availability on the duration of the gregarious phase of this maternal social spider, by subjecting laboratory-reared colonies (mother + offspring) either to a restricted or to an ad-libitum diet.

MATERIAL AND METHODS

Coelotes terrestris is a terricolous species, living under stones, bark of dead logs, etc., common in many European forests. It usually spins a tube opening at the ground surface through a small sheet web. The female lays 30 to 70 eggs. The young hatch after a 3-4 week incubation period. They stay for about one month in the tube, feeding on prey caught by the female. Insects are captured on the sheet-web (diameter 10-20 cm), carried into the tube, then dropped in the vicinity of the young. Feeding of young through regurgitation, though suspected by Tretzel (1961) has never been demonstrated. The offspring stay with their mother for about one month (34 days according to Tretzel 1961), and exhibit a clumping tendency even in the mother's absence (Horel, Roland and Leborgne 1979, Horel Leborgne and Roland 1982). Sometimes the mother dies before the offspring's dispersal, but the presence of a live mother does not prevent the offspring from dispersing.

Inseminated females, collected in beech forests around Nancy (Lorraine-France), were individually reared in the laboratory in glass boxes (20 x 20 x 12

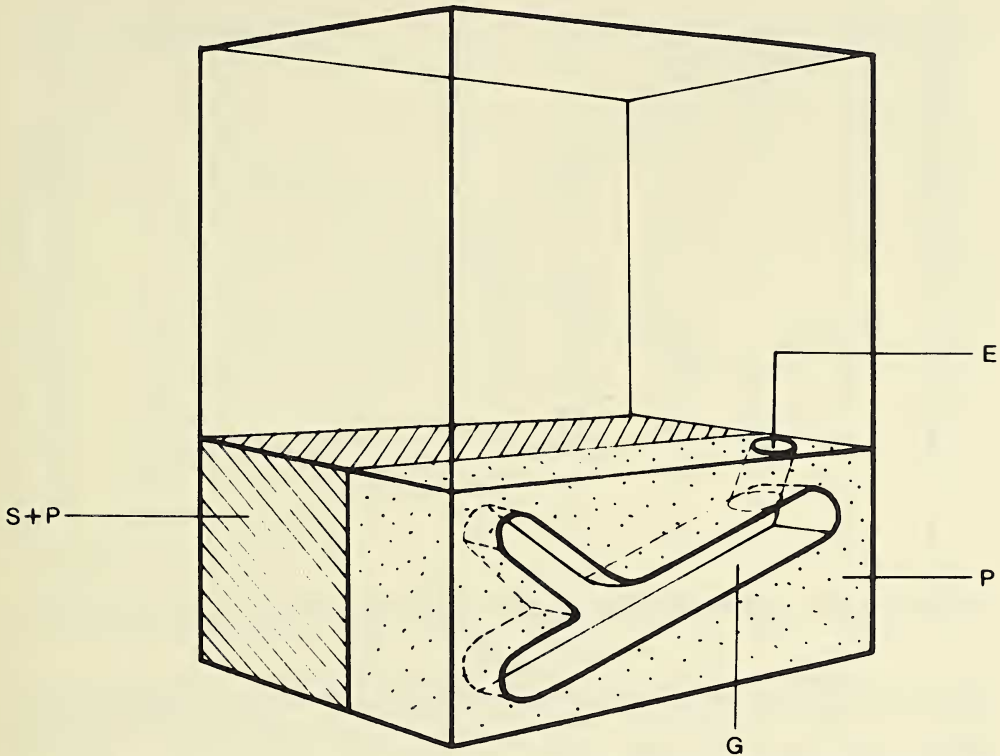


Fig. 1.—Rearing box. Dimensions: H = 20 cm, W = 20 cm, D = 12 cm, S + P = sand + peat, P = block of plaster, G = gallery, E = gallery's entrance.

cm) containing a mixture of sand and peat to facilitate humidification, and a block of plaster with a gallery where the female could spin its tube (Fig. 1).

The spiders were fed crickets (*Gryllus domesticus*, *Gryllus bimaculatus*). During the experiment, medium size (about 14 mg) cricket nymphs were provided exclusively. Such prey could easily be captured by the female (150-200 mg), but not by the young (max: 30 mg).

Predation was restricted to the mother to make easier the control of the colony's food intake. The effect of the young's predation is now under study.

After the spiderlings' emergence, colonies were randomly assigned to 2 treatments: 1. "Set +"; 10 colonies (median number of young: 37) were fed ad libitum. The number of live crickets was checked every day, and when necessary, adjusted up to 6 in each box. This set provided data to evaluate prey capture rate during development. 2. "Set -"; 9 colonies (median number of young: 36) had a restricted diet. They were provided only one nymph per week. Under such conditions, "set -" ate approximately 15 times less than "set +". The rearing boxes were carefully examined daily, and the positions of the spiderlings inside or outside the tube were checked.

RESULTS

Changes in colony food requirements.—A steady increase in the mean prey capture rate of the ad libitum fed "set +" was observed after the emergence of the

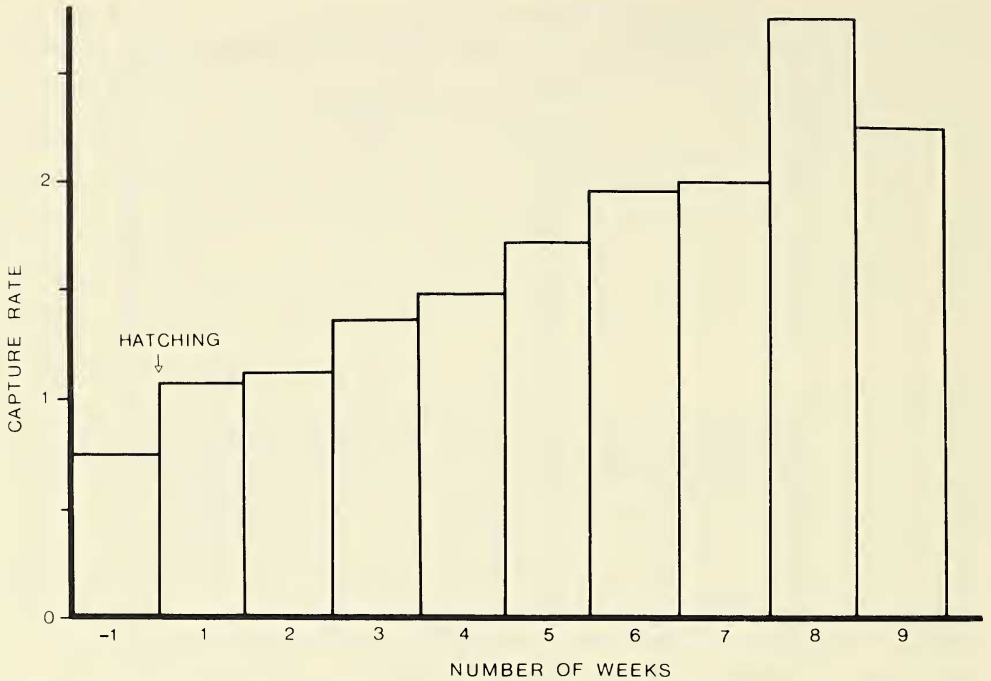


Fig. 2.—Developmental changes in the prey capture rate of ad-libitum fed colonies (Mean daily number of crickets captured during a week per colony). Statistical comparisons (sign test): Pre-emergence week versus post-emergence week 1: $p = 0.002$; Post-emergence week 1 versus post-emergence week 2: N.S.; Post-emergence week 1 versus post-emergence weeks 3-9: from $p < 0.05$ to $p < 0.001$.

young (Fig. 2). There was a significant difference between the pre-emergence week and the first post-emergence week (Sign test: $p = 0.002$). This increase in the capture rate can be considered as indicative of an increase in the spiderlings' food requirements, as other experiments under progress show that artificial suppression, or natural dispersal, of the offspring reduce the mother's prey capture rate to its pre-emergence level.

Extension of the colony in the gallery.—Owing to the difficulty of observation through the silk layer, it was not possible to determine the exact position of every spiderling in the gallery. Thus, the gradual expansion of the colony was estimated by the distance between the most distant visible spiderlings.

After emergence, the young spiders stayed close together, initially constituting a very tight aggregate, then extending more and more in the gallery as they got older (Fig. 3). Treatments did not differ in this respect (Sign test: N.S.).

Dispersal.—The difficulties of observation led us to choose as an index of dispersal the date when, for the first time, one spiderling was located outside the gallery during day-time. The accuracy of this index was tested by observing the dispersal of a colony of 20 spiderlings from a rearing-box introduced into a large enclosure (180 x 60 cm). Such an enclosure made it possible for the young to widely disperse, while still being easily spotted. When outside the gallery, the spiderlings went off as far as possible, and, once initiated, the process of going out never reversed (Fig. 4). So, the first appearance of a young spider outside the gallery can be considered to mark the beginning of dispersal.

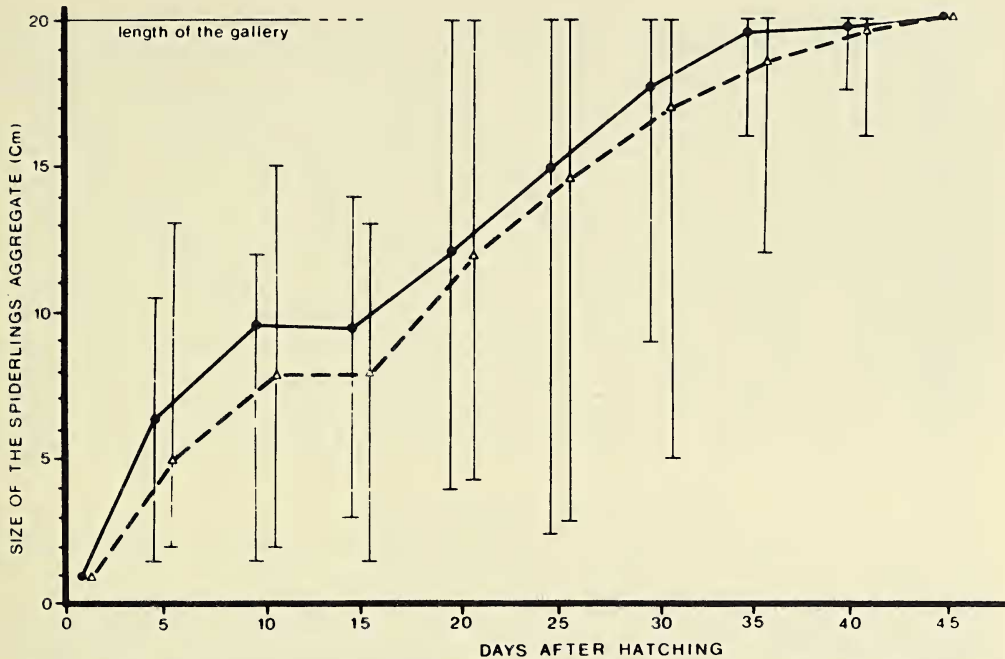


Fig. 3.—Expansion of the colony in the gallery (Mean size [in cm] of the aggregate every 5 days \pm range): Solid lines = "Set -" (Restrictively fed colonies, n = 9); Dotted lines = "Set +" (Ad-libitum fed colonies, n = 10).

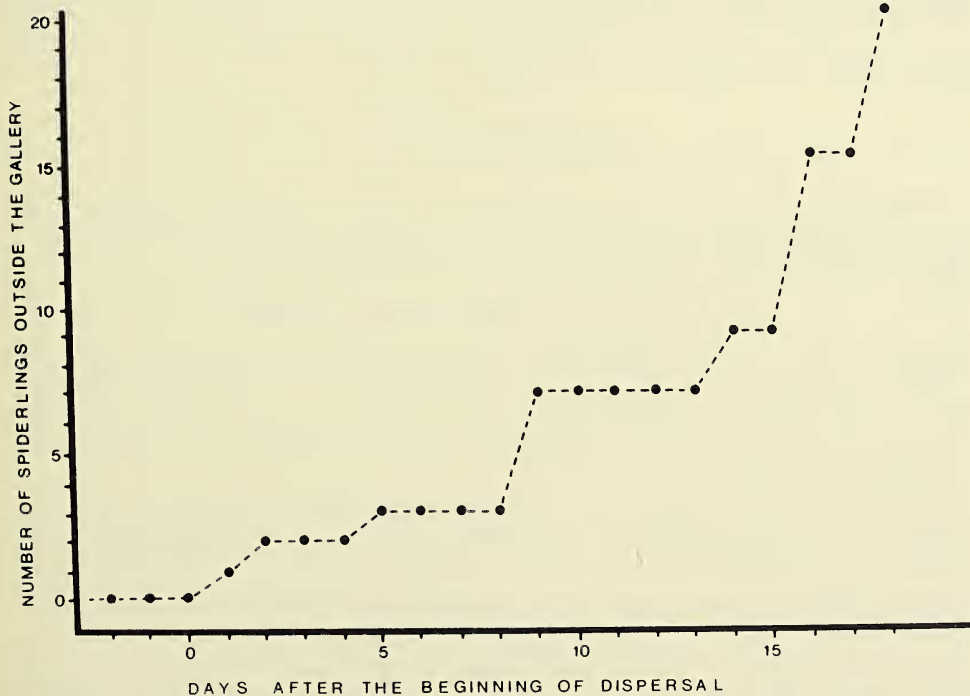


Fig. 4.—Dispersal of a colony of 20 spiderlings in a large enclosure (Day 0 is the day preceding the first spiderling's going out).

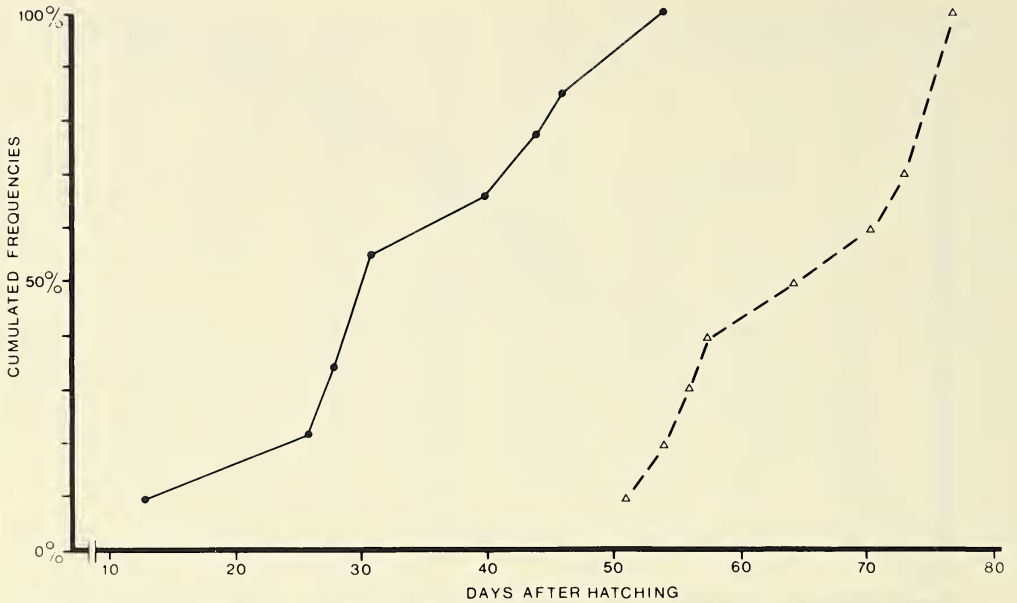


Fig. 5.—Cumulative distribution of the duration of the gregarious phase according to prey abundance in two sets of colonies: Solid lines = “Set -” (Restrictively fed colonies, $n = 9$); Dotted lines = “Set +” (Ad-libitum fed colonies, $n = 10$) (Mann and Whitney test: $U = 2$; $p < 0.001$).

Figure 5 represents the cumulative frequencies, in both sets, of the gregarious phase durations, i.e. the lapse of time between the hatching of the young from the egg-sac and the beginning of their dispersal. Young of the restricted diet set dispersed fairly earlier than those of the ad-libitum fed set (Mann-Whitney test $U = 2$, $p = 0.001$). The median gregarious period was 64 days in “set +”, whereas it was 31 days in “set -.”

DISCUSSION

This experiment shows, first, that the colony's food requirements increase along with the development of young. When these requirements eventually exceed the supply which can be obtained by the colony, the spiderlings abandon their communal behavior and disperse. Food shortage was produced in “set -” by the low number of prey items provided; however, the factors responsible for “set +” dispersal are not yet clearly known. Genetic factors cannot be ruled out entirely. Other factors concerning the predatory behavior of the mother are also unclear because of the limitations placed on the observation of her behavior by our experimental design.

We have shown that well-fed young dispersed significantly later than did underfed young. This indicates that the temporary social structure of *Coelotes terrestris* contains a certain degree of plasticity, because its duration can be modified by prey availability. Such a plasticity is an argument in favor of the familial or “maternal-social” origin of at least some spider societies (Krafft 1982).

The actual behavioral mechanisms related to dispersal of young are not yet clearly known. They might involve a fading of interattraction, or an increase in agonistic behavior induced by food competition, as observed in several solitary

or social species (Riechert 1976, 1978; Burgess and Uetz 1982, Rypstra 1985). These phenomena, as well as the development of mother-offspring interactions (namely during predatory activities), are currently under study in our laboratory.

It is very instructive to compare the results obtained with a maternal-social sheet-web spider and those obtained with *Metepeira spinipes*. This orb-weaver from Mexico, (as *Philoponella oweni*, Smith, 1983) may be solitary or live in groups according to the habitat's prey abundance. In field experiments, Uetz et al. (1982) demonstrated in *M. spinipes* a "flexible social spacing pattern and rapid responses to changes in prey availability." Thus, although differing in their geographical location, taxonomic position, web structure and type of social living, these species show a similar plasticity in their social organization, depending on prey abundance. Such a convergence is another argument in favor of a multiple origin of sociality in spiders, and of the significance of trophic factors (among other ecological factors) in these evolutionary events.

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